BIG-FRUITED BUCKTHORN, *SIDEROXYLON MACROCARPUM* (SAPOTACEAE), A LONG-FORGOTTEN GEORGIA ENDEMIC

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ABSTRACT

Bumelia macrocarpa Nutt. languished in obscurity for more than 150 years. Thomas Nuttall (1786-1859) collected this low shrub in 1830 and described it in 1849. Asa Gray relegated it to the synonymy of *B. lanuginosa* (Michx.) Pers. in 1886, apparently due to the lack of subsequent collections and without seeing any material of Nuttall's plant. In 1940 Robert Clark identified type material of *B. macrocarpa* as *B. reclinata* (Michx.) Vent., failing to notice the fact that more than one species had been mounted on the sheet, with only one small fragment actually representing *B. macrocarpa*. Since *Bumelia* Swartz is now considered to be a synonym of *Sideroxylon* L., the restoration of this distinctive species, endemic to southeastern Georgia (U.S.A.), requires a new combination, *S. macrocarpum* (Nutt.) J.R. Allison.

RESUMEN

Bumelia macrocarpa Nutt. languideció en la oscuridad durante más de 150 años. Thomas Nuttall (1786-1859) coleccionó este arbusto bajo en 1830 y lo describió en 1849. Asa Gray lo relegó a la sinonimia de *B. lanuginosa* (Michx.) Pers. en 1886, aparentemente debido a la carencia de colecciones subsiguientes y sin ver ningún material de la planta de Nuttall. En 1940 Robert Clark identificó el material tipo de *B. macrocarpa* como *B. reclinata* (Michx.) Vent., al no notar el hecho que se había montado en la lámina más de una especie, con un solo fragmento pequeño que representa en realidad *B. macrocarpa*. Puesto que *Bumelia* Swartz se considera actualmente un sinónimo de *Sideroxylon* L., la restauración de esta especie distintiva, endémica al sureste de Georgia (EEUU), requiere una nueva combinación, *S. macrocarpum* (Nutt.) J.R. Allison.

INTRODUCTION

Among the genera of woody plants listed in the work that launched the modern system of binomial nomenclature, Linnaeus' *Species Plantarum* of 1753,[1] was *Sideroxylon* L. (<Gk. *sideros*, iron + *xylon*, wood). In the second edition, of 1762, he named the first *Sideroxylon* from the southeastern United States, *S. lycioides* L., and in 1767 a second one, *S. tenax* L. The species of the temperate southeastern U.S.A. (one species extending sparingly to Arizona), spiny shrubs or small trees with short styles and finely reticulate, often fascicled leaves, were usually treated under the genus *Bumelia* Swartz for two centuries following the latter's segregation from *Sideroxylon* in 1788 (e.g. de Candolle 1844; Gray 1886; Small 1933; Wood & Channell 1960; Godfrey 1988). An early exception was

[1]For more nomenclatural citations, see Pennington 1990.

Michaux's (posthumous) description of two species from Georgia in 1803, *S. lanuginosum* Michx. and *S. reclinatum* Michx. In the following pages, I use one or the other generic name interchangeably as deemed appropriate, mostly using *Bumelia* when referring to works which used it, *Sideroxylon* when discussing more recent treatments or concepts. Whatever the botanical name, "buckthorn" has been in use as a vernacular name for these plants for many years (Gray 1878).

All four of these species were restored to their original nomenclature when T.D. Pennington (1990, 1991) synonymized *Bumelia* under *Sideroxylon* as not constituting a natural (monophyletic) group. For his coverage of the hardy taxa of the southeastern U.S.A., Pennington (1990) was explicit that he relied almost exclusively on Arthur Cronquist's (1945, 1949) publications on *Bumelia*. Although at least two dozen species had been named from the U.S. in the 150 years after Michaux, Cronquist (1945) opined that "not a single valid species of *Bumelia* seems to have been described from the United States since the appearance of Michaux's flora in 1803." Four years after this remark, however, Cronquist (1949) described *B. thornei* Cronq., from collections he had seen from southwestern Georgia. Relying on Cronquist's conservative treatment simplified Pennington's (1990) task, as this meant only five temperate species of *Sideroxylon* to be treated, the two each of Linnaeus and Michaux, and *S. thornei* (Cronq.) Pennington.[2]

However, another monograph covering these species (except *Sideroxylon thornei*), by Robert Clark (1942), had been published just three years before Cronquist's. I consider these almost polar opposites, Cronquist's a "lumper's" treatment and Clark's that of a "splitter." For Pennington to have weighed the validity of all the taxa recognized by Clark was clearly beyond the intended scope of Pennington's work, which was focused on the Neotropical members of *Sideroxylon* and other genera of Sapotaceae.

In Clark's revision of the U.S. species of *Bumelia*, he recognized 14 species as well as 2 varieties each of *B. lanuginosa* (Michx.) Pers. and *B. lycioides* (L.) Pers., not including their type varieties. He accepted *B. texana* Buckl. and *B. rufa* Raf., raised *B. lanuginosa* var. *anomala* Sarg. and var. *rigida* A. Gray to species rank, and accepted most of the species named by J.K. Small. Despite Clark's splitter's perspective, he did, without comment, reduce to synonymy under *B. reclinata* (Michx.) Vent. one taxon that had been accepted by Asa Gray in the

[2]A more distantly related, non-hardy "*Bumelia*" of the Caribbean has long been known from the warmer areas of the southeastern U.S.A., in southern Texas and peninsular Florida. It has been treated under several names, e.g. *B. cuneata* Swartz (misapplied by Gray), *B. angustifolia* Nutt. (nom. superfl., published 24 years after the next), *B. celastrina* Kunth, and now *Sideroxylon celastrinum* (Kunth) T.D. Pennington. The still more distantly related *S. salicifolium* (L.) Lam. and *S. foetidissimum* Jacq. are also known from peninsular Florida; they were treated by Cronquist (1945, 1946) as *Dipholis salicifolia* (L.) A. DC. and *Mastichodendron foetidissimum* (Jacq.) Lam., respectively.

first edition of the *Synoptical Flora* (1878): *B. lanuginosa* var. *macrocarpa* (Nutt.) A. Gray. Clark's decision was no doubt based on his examination of the only specimen (Fig. 1) known to exist, at least in North America, that was identified as *B. lanuginosa* var. *macrocarpa* or as its basionym, *B. macrocarpa* Nutt. The specimen shows no sign of having been examined by Cronquist, who, like Clark, listed *B. macrocarpa* in the synonymy of *B. reclinata*.

I have concluded that Clark's annotation of the sheet in question as *Bumelia reclinata* resulted from an insufficiently thorough examination of it. The sheet is in fact a mixture, bearing four fragments correctly identified by Clark as the glabrate *B. reclinata*, and a single fragment with smaller, thinly but persistently strigose leaves corresponding to the protologue (Nuttall 1849) of *B. macrocarpa*. This fragment also matches plants known today from the same region and sandy, upland habitat indicated in Nuttall's protologue.

In this paper I restore this taxon, a Georgia endemic (Fig. 2), to species status. Although the specific epithet *macrocarpa* has been used within other Sapotaceous genera, it does not appear to be preoccupied in *Sideroxylon*. Therefore the plant's transfer to *Sideroxylon* requires only a new combination. As this taxon has never received a detailed description, I provide one, constructed to parallel those in Pennington 1990.

TAXONOMIC TREATMENT AND DESCRIPTION

Sideroxylon macrocarpum (Nutt.) J.R. Allison, comb. nov. (**Figs. 3–5**). BASIONYM: *Bumelia macrocarpa* Nutt. Sylva 3:34. 1849. *Bumelia lanuginosa* var. *macrocarpa* A. Gray. Syn. Fl. 2(1): 68. 1878. TYPE: U.S.A. GEORGIA (according to the protologue, "sandy hills not far from the Altamaha"): *Nuttall s.n.* (LECTOTYPE [Fig. 1]: PH, accession no. 1030290, the small fragment at top left *only*, which pierces Nuttall's original label).

Plants soboliferous shrubs less than 1 m high, usually under 0.5 m; geoxylic (woody underground) stems much longer than the aerial, to at least 10 mm thick; aerial (leafy) stems 0.5–2(–3) mm thick, often with thornlike branchlets bearing reduced leaves. Long shoots (elongation or leader) tan or reddish-brown and tomentulose when young, the hairs blondish or some of them ferruginous, soon glabrate, gray with age, armed at most nodes with slender, slightly curved, sharp thorns (2–)2.5–13(–20) mm long; some thorns becoming short spur-shoots. **Leaves** tardily deciduous, coriaceous, spirally alternate and spaced at first, soon becoming fascicled on short shoots, internodes (1–)2–12(–21) mm long (imperceptible on short [spur-] shoots); petioles (0.5–)1–3(–5) mm long, channeled, pilosulous; blades dark green above, paler beneath, narrowly oblanceolate to obovate or spatulate, or broadly elliptic to suborbicular, especially on some spur-shoots, (0.3–)1–4(–5.2) cm long, (0.2–)0.4–1.5(–2.1) cm wide, glabrate above, persistently and rather sparsely strigose beneath, occasionally virtually glabrate, the hairs blond or rarely slightly rufous; apex obtuse or rounded, sometimes retuse, base cuneate or acute; venation brochiodromous or eucamptodromous,

FIG. 1. The only specimen found at PH of *Bumelia macrocarpa*, labeled as *Bumelia lanuginosa* var. *macrocarpa*. Inset, placed over a large blank space on the sheet: the only material of genuine *B. macrocarpa* (=*Sideroxylon macrocarpum*) on the sheet, bearing three persistent, puberulent leaves of the previous season, and several densely hairy leaves just beginning to expand. The four other fragments are *S. reclinatum* s. str.

without a marginal vein, midrib flat or slightly sunken on the upper surface, secondary veins mostly 5–8 pairs, ascending, arcuate, intersecondaries usually moderately long; tertiaries reticulate-areolate on both surfaces. **Flowers** bisexual, actinomorphic, in axillary (1–)2–15(–18)-flowered fascicles on growth of the preceding year. Pedicels 1–3(–5.5) mm long, pubescent. Sepals (4–)5(–6), unequal (outer pair slightly shorter) (2.1–)2.5–3 mm long, suborbicular to ovate, sparsely to moderately pale sericeous-tomentulose, margins scarious, apex rounded to subtruncate or slightly retuse. Corolla (4)5(6)-merous, creamy white; tube (0.7–)

1–1.3 mm long, lobes (1.8–)2.4–3(–3.5) mm long, erose; medial lobe-segment erect in anthesis, ovate to suborbicular, apex rounded, lateral segments (appendages) infolded in anthesis, obtuse or sometimes acute, (1.5–)1.8–2.3(–3.1) mm long, lanceolate to nearly oblong. Stamens (4–)5(–6), filaments 1–2 mm long, anthers 1.1–1.3(–1.5) mm long, lanceolate. Staminodes (4–)5(–6), infolded, (1.2–)1.3–1.8(–2.0) mm long, reaching (1/3) 1/2–2/3 the length of the corolla midlobes and exceeded by the lateral lobes, lanceolate to ovate, apex acute to rounded. Ovary broadly ellipsoid, glabrous or medially villosulous. Style 1.0–1.3(–1.5) mm long after anthesis, glabrous; style-head simple. **Fruit** smooth, black, somewhat lustrous, ellipsoid to subglobose, often tipped by the persistent style-base, when fresh 9–12(–14) mm long, 8.5–10 mm wide, apex and base rounded, pericarp ca. 2 mm thick, fleshy, sweet. Seed solitary, (7.3–)8–9 mm long, 5.5–7 mm wide, ellipsoid or obovoid, with truncate base. Testa hard, smooth, evenly brown, moderately lustrous, 0.5–1 mm thick; scar basal, in two parts, a roughly semicircular area 2–3 mm across and a smaller, deltate to lunate abaxial area, the two sometimes joining.

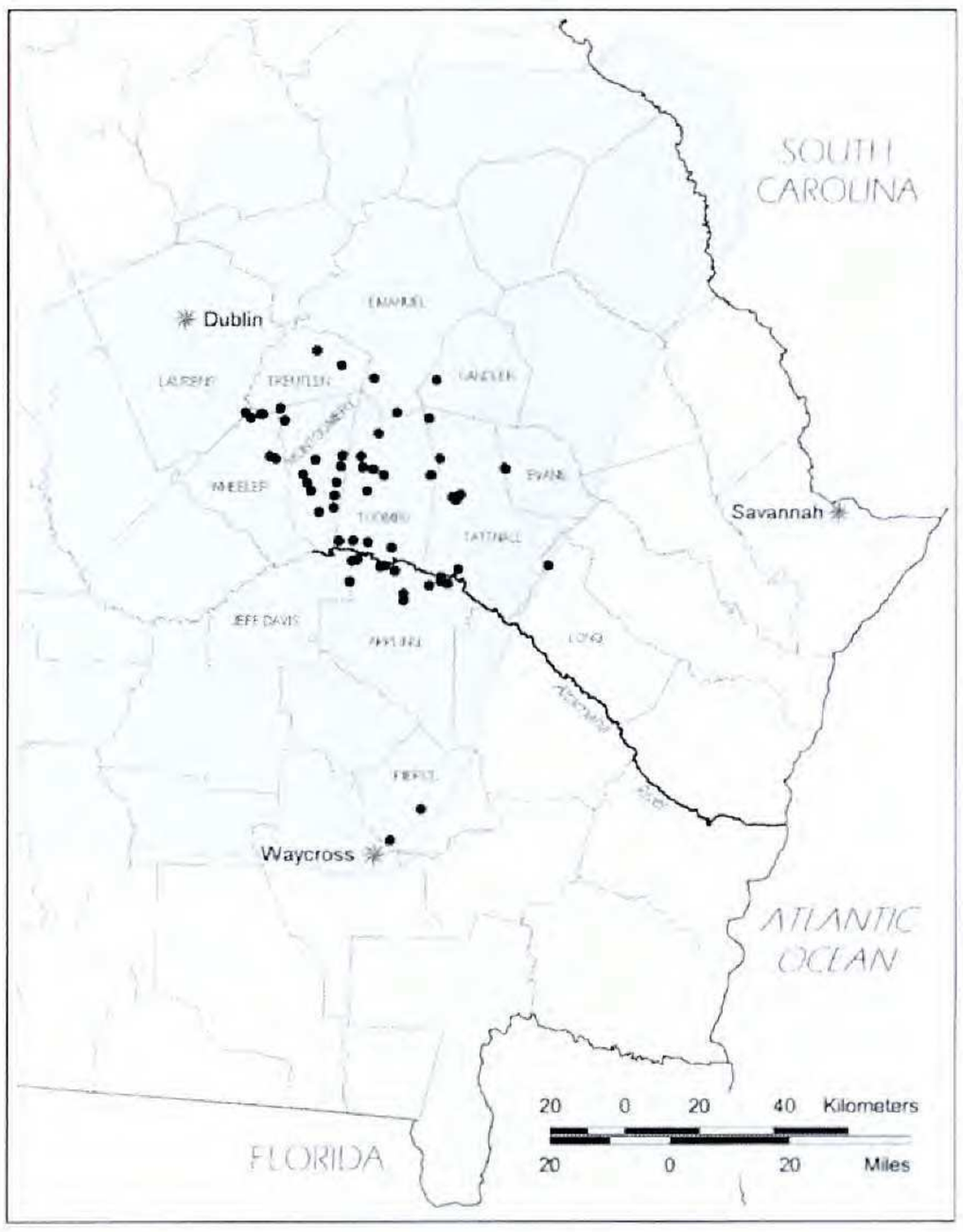

FIG. 2. County outline map of southeastern Georgia showing known localities of *Sideroxylon macrocarpum* (dots), the Altamaha River, and three cities. The shaded area corresponds to the approximate eastern extent of the Altamaha Formation, as mapped in Huddlestun 1988.

Phenology and habitat.—Flowering late May through June, or sporadically through September. Sandy, well-drained, partly open, pine-oak woodlands and pine-oak scrub, southeastern Georgia, U.S.A.

Additional collections examined: **UNITED STATES. GEORGIA: Appling Co.:** Co. Rd. 537, 20 Sep 1993, *Nordman & Tassin s.n.* (GA); Co. Rd. 368, 20 Sep 1993, *Nordman & Tassin s.n.* (GH); Co. Rd. 363, 20 Sep 1993, *Nordman & Tassin s.n.* (NY); 25 Jul 1996, *Allison & Tassin 9352* (FSU, NCU); just SE of Hatch nuclear power plant, 26 May 1999, *Nelson & Kennemore 20559* (USCH). **Candler Co.:** GA 46, 27 Sep 1994, *Allison 8606* (USCH); 29 May 1996, *Allison 9203* (FSU, GA); 10 Sep 2005, *Allison 13782* (CLEMS, VSC). **Emanuel Co.:** 25 mi S of Swainsboro, 24 Apr 1937, *Henry 1019* (NY); GA 46, 29 May 1996, *Allison 9200* (JSU); US 1, 10 Jul 1995, *Allison 8914* (FLAS, UNA, USCH); 29 May 1996, *Allison 9202* (FSU); 16 Jun 1999, *Allison 12022* (GA, GH, MICH, TAMU, TENN, TROY). **Evans Co.:** 1.8 mi NW of Bellville, 7 Apr 1997, *Van de Genachte et al. s.n.* (PH); 16 Sep 2001, *Allison 13043* (GA, GH, NCU, NY, US); 11 Sep 2005, *Allison 13796* (GA, VDB); 1.6 mi NW of Bellville, *Allison 9764* (FSU, MO, USCH). **Jeff Davis Co.:** Bullard Creek WMA, 8 May 1997, *Allison 9768* (FSU); 8 Jun 1999, *Allison 11988* (AUA, BRIT, CLEMS, FLAS, GA, GH, JSU, MICH, MO, NCU, NY, PH, TAMU, TENN, TEX, TROY, UNA, US, VDB, VSC); 29 Sep 1999, *Allison 12220* (GA); near Perry Miller Rd., immediately W of Appling Co. line, 26 May 1999,

FIG. 3. *Sideroxylon macrocarpum* specimen-collage, from collections at GA, all to same scale. **A.** Two (leafy) aerial shoots arising from one (incomplete) sparsely-rooted geoxylic stem, *Allison 11988*. **B.** Part of stem with larger than normal leaves (to 5 × 2.1 cm), *Allison 8607*. **C.** Flowering stem, *Allison 12040*. **D.** Stem fragment bearing mature fruits, *Allison 13048*. **E.** Stem fragment with a leaf shape more typical of *S. rufohirtum*, *Allison 13043*. **F.** Stem with thornlike branchlets bearing reduced leaves, *Allison 12022*.

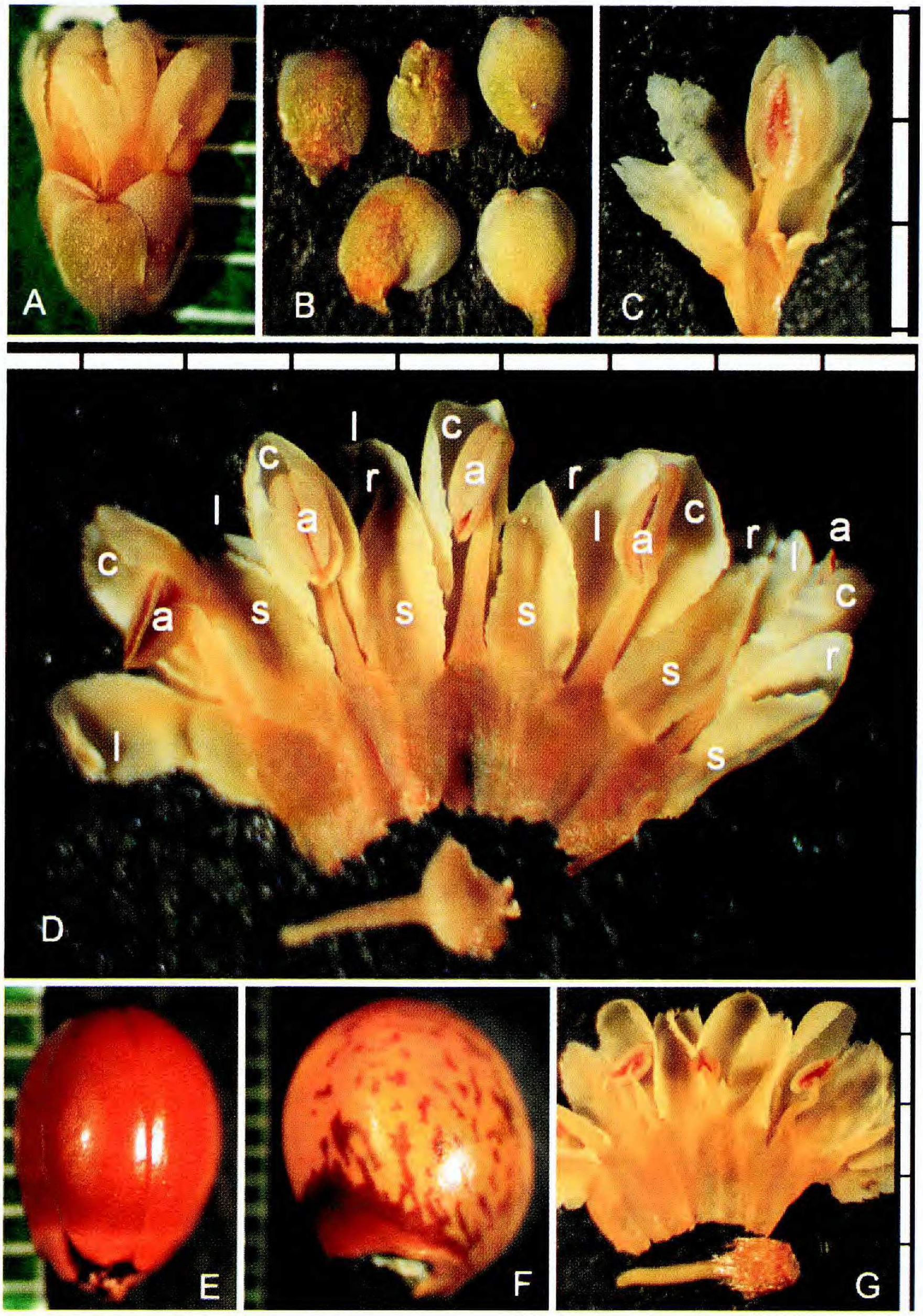

FIG. 4. *Sideroxylon* sample dissections and seeds, from collections at GA (against millimeter rulers or with bars marked in millimeters). **A–D,** from rehydrated flowers of *S. macrocarpum* (*Allison 9203*). **A.** Flower. On the right side of the corolla the tripartite division of a corolla-lobe is evident. **B.** Sepals, the outer two greener and slightly smaller (same scale as A). **C.** Part of a flower; from left to right: a staminode, a left corolla-lobe appendage, a corolla-lobe and stamen, and a right corolla-lobe appendage. **D.** Above, spread corolla and androecium: a = anther, s = staminode, c = corolla-lobe, l or r = left/right appendage of corolla-lobe (one of the latter completely obscured by a corolla-lobe). Below, upper portion of pistil: style and (glabrous) summit of ovary. **E.** Seed of *S. macrocarpum* (*Allison 13048*). **F & G,** comparative material of *S. rufohirtum*: **F.** Variegated seed (*Allison 12292*). **G.** Floral dissection: the proportionately larger staminodes mostly obscuring the corolla-lobe appendages (apex of one is visible at 11 o'clock), and the ovary rufous-hairy (*Allison & Anderson 9918*).

Nelson & Kennemore 20576 (USCH). **Laurens Co.:** GA 19, 21 Aug 1996, *Allison 9404* (AUA, BRIT, FSU, US, USCH); 18 Jun 1999, *Allison 12040* (GA, MO). **Long Co.:** Ft. Stewart, N of GA 144, near Tattnall Co., 25 Aug 1992, *Zebryk et al. 598* (GA); 8 May 1997, *Allison 9766* (USCH, VSC); 9 Jun 1997, *Allison 9876* (FSU, GA, NY). **Montgomery Co.:** Co. Rd. 171, 21 Aug 1996, *Allison 9408* (USCH); US 280, 21 Aug 1996, *Allison 9409* (FSU, TEX); GA 135, S of Alston, 22 Aug 1996, *Allison 9411* (GA); GA 135, 3 1/2 mi N of Alston, 7 May 1997, *Allison 9746* (CLEMS, JSU, PH). **Pierce Co.:** N of Satilla R., near US 82, 6 Jul 1959, *Cypert 211* (GA); 2 mi N of Blackshear, 9 Nov 1994, *Allison 8754* (FSU); 29 Sep 1999, *Allison 12228* (FLAS, GA, TENN, USCH). **Tattnall Co.:** near Reidsville, 24 Jun 1903, *Harper 1851* (GH, 2 sheets; MO; NY); NW of Reidsville, 27 May 1957, *Broughton s.n.* (GA); E of Ohoopee R., near GA 292, 29 Aug 1985, *Rayner & McCartney 2401* (USCH); May 1987, *McCartney s.n.* (GA); Gordonia Alatamaha State Park, 20 Sep 1993, *Nordman et al. s.n.* (US); GA 57/121 near N limits of Reidsville, 17 Oct 1993, *Nordman et al. s.n.* (MICH); 27 Sep 1994, *Allison 8607* (GA); 30 May 1996, *Allison 9207* (FLAS, FSU, TAMU, TROY). **Toombs Co.:** 3.8 mi N40°W of Lyons, 24 Oct 1952, *Duncan & Hardin 14622* (GA); Co. Rd. 364 at Co. Rd. 279, 25 Aug 1993, *Nordman s.n.* (BRIT); 0.2 mi SW of Old Smyrna Cem., 25 Aug 1993, *Nordman & Tassin s.n.* (MO); GA 86 near Pendleton Creek, 17 Sep 1993, *Nordman et al.* (PH); U.S. 280, 12 Sep 1995, *Allison 8978* (USCH, VSC); GA 15, 22 Aug 1996, *Allison 9418* (GA). **Treutlen Co.:** Co. Rd. 167, 5 Oct 1994, *Allison 8662* (BRIT, JSU, MO, NCU, NY); 29 May 1996, *Allison 9199* (FSU, GA, VDB); GA 86, 23 Aug 1996, *Allison 9430* (USCH). **Wheeler Co.:** GA 46, 4 Jul 1996, *Snow s.n.* (GA); 26 Jul 1996, *Allison & Snow 9356* (GA); GA 19, 21 Aug 1996, *Allison 9406* (AUA, FSU, TEX, US, USCH); 17 Sep 2001, *Allison 13048* (GA, MICH, UNA).

HISTORY OF TAXON

Nuttall's choice of epithet, *macrocarpa*, "large-fruited," was surely intended to contrast with the small fruit of the only other relatively low and small-leaved species known to him from the U.S.A., *Bumelia reclinata*. His treatment of what I call *Sideroxylon macrocarpum* is a fairly accurate, if incomplete, description of the plant known today from many more observations, made throughout the growing season. The protologue is brief enough to be quoted here in its entirety:

> LARGE-FRUITED BUMELIA.
>
> BUMELIA MACROCARPA, depressa, ramis gracilibus valde spinosis, spinis elongatis tenuibus subrecurvis, foliis parvulis cuneato-lanceolatis obtusis junioribus lanuginosis, demum subglabris concoloribus; drupa maxime ovali.
>
> This very low bushy species, allied to *B. reclinata*, I give (though from very imperfect specimens) to complete the history of our species of the genus. The twigs are very slender, at first pubescent, covered with a grey bark, and with the spines long and slender as needles. The leaves, before expansion, are exceedingly lanuginous, and always small, with very short petioles, at length nearly smooth. The fruit is edible, and as large as a small date! I found this species on the sandy hills not far from the Altamaha, in Georgia, in winter, and therefore do not know the flower. It does not grow more than a foot high, and the leaves are little more than half an inch long.

Nuttall's collection was probably made in 1830. According to Graustein (1967), it is only in that year that Nuttall visited the area of Georgia where the plant is known to grow today. She also indicates that he was in the Florida Pan-

FIG. 5. *Sideroxylon macrocarpum* in life. Above: unusually extensive patch (10 m^2 or more); source of *Allison 9764*, in sandy powerline right-of-way, Evans Co., 8 May 1997; note young *Pinus palustris*, top center. Below, same locality and date: sandy, well-drained habitat, with gopher tortoise burrow (just left of center) and a small clump of *S. macrocarpum* (indicated by arrow). Inset: branch with leaves, thorns, and a mature fruit, prior to collection as part of *Allison 12228*, Pierce Co., 29 Sep 1999.

handle early in March of 1830, subsequently crossed the Altamaha River[!] en route to Savannah, where he departed the Southeast by ship, and that he was back in Pennsylvania by April 17. As Nuttall indicated that he had seen the buckthorn only in winter, it is likely that the collection was made in mid-March.

When Gray (1878) reduced *Bumelia macrocarpa* to *B. lanuginosa* var. *macrocarpa*, not quite three decades after Nuttall described it, he added, "To be rediscovered." Presumably the lack of subsequent collections was a major factor when Gray later (1886) dropped his variety *macrocarpa*, listing *B. macrocarpa* in the synonymy of *B. lanuginosa* and stating that Nuttall's plant "must be this or the preceding" [*B. tenax* (L.) Willd.]. Seemingly, Gray came to regard Nuttall's plant as likely to have been merely an aberrant form of a previously described species, and eliminated *B. reclinata* from consideration due to the latter's small fruit and typically glabrate leaves.

A second collection of *Sideroxylon macrocarpum* would not be made until the early years of the 20th Century, when the region of Georgia to which Nuttall's plant is endemic was explored botanically by Roland M. Harper for his doctoral dissertation, published as *A Phytogeographical Sketch of the Altamaha Grit Region of the Coastal Plain of Georgia* (Harper 1906). "Altamaha Grit" refers to a stratigraphic unit now called the Altamaha Formation (Huddleston 1988). Harper cited *Harper 1851* under *Bumelia reclinata*, and listed additional sites from sandhills or dry pine barrens in Tattnall, Montgomery, and (present day) Wheeler Counties. The latter were presumably sight records, as no specimens were cited. Given their geographic location and habitat, Harper's three sight records of "*B. reclinata*" almost certainly also represent *S. macrocarpum*. Another collection is known from the first half of the 20th century, *Mrs. J.N. Henry 1019* (NY), from 1937. Its label bears no determination except for the word *Bumelia*, handwritten anonymously just above the label, and was otherwise never annotated.

The next three collections of *Sideroxylon macrocarpum* known to me are at GA: *Duncan & Hardin 14622* (in 1952, Toombs County), *Broughton s.n.* (1957, Tattnall Co.), and *Cypert 211* (1959, Pierce Co.). Wilbur Duncan identified his and Broughton's specimens as *Bumelia reclinata*, Cypert's as *B. lanuginosa*. These specimens were annotated by Cronquist in 1970, two of them simply as "*Bumelia thornei* Cronq." Cronquist elaborated slightly in his annotation of *Duncan & Hardin 14622*: "An unusual specimen which may perhaps best be associated with *B. thornei*." The habitat information supplied on the labels indicated that all three collections came from dry, sandy habitats. That they came from such habitats presumably posed no problem for Cronquist, since in naming *B. thornei* he had (erroneously) cited the habitat of the type (*Thorne 7345*, GA) as "*dry* [my emphasis, here and in the next quotation] live oak woods by cypress swamp" (Cronquist 1949). However, this conflicts with the habitat given by Robert Thorne himself (1949) for the type locality, namely "*moist* live oak woods at

edge of cypress swamp." Furthermore, Thorne (1949, 1954) gave the habitat of the species as a whole as "sandy, moist, open meadows or woods." Cronquist's mis-annotations of 1970 would have significant consequences.

The paucity of occurrences known for *Bumelia thornei* was undoubtedly the primary reason for its listing, in August 1977, as an endangered species under provisions of the Georgia Wildflower Preservation Act (Patrick et al. 1995). A month later McCollum and Ettman (1977) published a treatment of all the species then protected under that statute, with a description, Georgia range map, and line drawing of each. This government publication was made available free of charge and had wide distribution within the state. In it *B. thornei* was characterized as "a small, thorny shrub up to 1.5 m tall," that was found "in dry, live oak woods and scrub oak sandhills." Clearly their concept of *B. thornei* derived from Cronquist's original, somewhat faulty description and from at least one of his 1970 annotations, of *Broughton s.n.*, whose label gave the habitat as "scrub oak sandhills."

For more than ten years following McCollum and Ettman 1977, *Bumelia thornei* was considered by most botanists in the Southeast to be a low shrub of dry habitats. For example, in 1985 Robert B. McCartney reported to the Georgia Department of Natural Resources (GaDNR) his finding of a "new *Bumelia thornei* location," in Tattnall County (correspondence in files of the Natural Heritage Program of the GaDNR). In March of 1987 McCartney led a small group of botanists, myself included, to this population, which corresponded perfectly in habit and habitat to the treatment of *B. thornei* in McCollum and Ettman 1977. At this point Nuttall's *B. macrocarpa* had been languishing in synonymy for just over a century and completely forgotten by Georgia botanists.

Not surprisingly, knowledge gained in the decades subsequent to Clark 1942 and Cronquist 1945 supports a taxonomy of this group of species somewhere between the extremes represented by those two workers. To be fair to Cronquist, he was frank that the firmness of his taxonomic judgments was proportionate to the number of herbarium specimens available to him. The taxa named post-Michaux were usually represented by few collections. For some of these, rather more material has of course proved helpful, especially when combined with significant field experience with the plants, which neither Clark nor Cronquist could claim.

In contrast, Robert Godfrey had considerable experience with the group as *living* plants. For example, he is credited with the earliest known collection of *Sideroxylon thornei* from Florida, made in 1982 (Anderson 1988). Informed by his field experience with two taxa that had been treated by Cronquist (1945) as *Bumelia reclinata* var. *rufotomentosa* (Small) Cronq. and *B. tenax* f. *anomala* (Sarg.) Cronq., Godfrey (1988) restored them to species rank, as *B. rufotomentosa* Small and *B. anomala* (Sarg.) Clark. In this work Godfrey added new precision to their descriptions and discussed them in some detail, with line drawings of

each by Melanie Darst. Both of these buckthorns, however, had specific epithets that were preoccupied in *Sideroxylon*, so their eventual transfer to that genus at the rank of species required new names: *S. rufohirtum* Herring and Judd (1995) for *B. rufotomentosa*, and *S. alachuense* L.C. Anders. (Anderson 1997) for *B. anomala*.

In the same work, Godfrey revised the description of *Bumelia thornei*, giving the normal height (accurately) as around 2 1/2 meters, with a maximum plant height of 6 meters. He also described its fruits as larger than those of *B. lanuginosa*, whereas Cronquist (1949) in the *B. thornei* protologue had erroneously stated precisely the opposite.[3] Godfrey also correctly made *B. thornei* a wetland plant, giving the habitat as "woods bordering ponds (and creeks?), apparently where some surface water stands during wet seasons."

In 1988 McCartney observed *Bumelia thornei* at its type locality in Early County, Georgia (note in files of Georgia Natural Heritage Program) and, as his long, handwritten annotation on a 1985 collection (*Rayner & McCartney 2401*, USCH) makes clear, he realized that the often tall shrub of wetland habitats upon which *B. thornei* was founded could hardly be synonymous with the low plant of well-drained, sandy habitats portrayed in McCollum and Ettman 1977.

Angus Gholson showed me to the type locality of *Bumelia thornei* in May of 1990. Later that year I found a number of additional localities for genuine *B. thornei*, including several county records (Anderson 1996). Unaware of McCartney's observations, I came to the same conclusion, that *B. thornei* was not conspecific with the low plant of dry places in southeastern Georgia. The following year I provided a corrected description of *B. thornei*, in an update of *Georgia's Protected Plants* (McCollum & Ettman 1991), as a tall shrub of wetland habitats, known in Georgia (then) only from the southwestern part of the state.

This begged the question of what to call the low, large-fruited plant of dry, sandy habitats of south*eastern* Georgia. The combination of large fruit and comparatively small leaves with patchy, persistent hairs beneath, as well as the habit and habitat, invited comparison with one of the taxa restored to species status in Godfrey 1988: *Bumelia rufotomentosa* [*Sideroxylon rufohirtum*], considered to be endemic to north peninsular Florida. For example, McCartney's 1988 typewritten annotation of *D.A. Rayner & R. McCartney 2401* (USCH) states, "The Tattnall County material most resembles *B. rufotomentosa* from central Florida

[3]The treatments of Small (1900), Clark (1942), Cronquist (1945, 1949) and others based almost exclusively on herbarium collections contain errors regarding (mature) fruit size; sometimes the upper limits are given as too large, apparently based on the inclusion of misidentified material, sometimes too small, due to misjudging the state of maturity of unripe fruit on older, discolored specimens. Small, for example, described his *Bumelia rufotomentosa* (*Sideroxylon rufohirtum*) as having slightly smaller fruits than *B. reclinata*, when in fact they are distinctly larger at maturity.

which occurs in similar habitat but has more orbicular, persistent leaves. May represent a new taxon!"

In the early 1990s Carl Nordman, during surveys of rare species and natural communities of the Altamaha River basin for The Nature Conservancy of Georgia, found several new localities for the seemingly anonymous *Sideroxlon* in Appling, Pierce, Tattnall and Toombs Counties; vouchers for eight of these have been cited herein. I also maintained an interest in the plant, looking for it whenever my work for the GaDNR took me to the southeastern part of the state and making the first collections from Candler and Treutlen Counties. In 1996–97, I conducted for the GaDNR, with funding from the U.S. Fish and Wildlife Service, a status survey of *Sideroxylon thornei* and of the low plant of sandy places that had been mistakenly included within it (Allison 2000). Soon thereafter I shared my findings and some specimens with an authority on *Sideroxylon*, Loran Anderson. Informally, in an abstract, we indicated our intention to name the plant *S. duncanorum* (Allison & Anderson 1998). The proposed specific epithet was to commemorate a lifetime of service to southeastern botany on the part of the late Wilbur H. Duncan and of his wife and work partner, Marion B. Duncan. I plan, instead, to name another Georgia endemic shrub (of the Lamiaceae) in their honor.

While working up the manuscript for the "new species" of *Sideroxylon*, I came across the name *Bumelia macrocarpa* Nutt. among synonyms of *B. reclinata* listed in Clark 1942. Nuttall's choice of an epithet meaning "large-fruited" demanded further inquiry, as this name would be very appropriate for the Georgia endemic. Furthermore, I recalled that Nuttall collected the type of *Arenaria brevifolia* Nutt. ex Torr. & A. Gray [=*Minuartia uniflora* (Walt.) Mattf.] from Tattnall County, Georgia (Harper 1904), placing him in the vicinity of extant locations of the supposedly undescribed Georgia buckthorn.

In May of 2005 I examined the only sheet (Fig. 1) of Nuttall's *Bumelia macrocarpa* at the Academy of Natural Sciences, Philadelphia (PH). It bears five fragments of *Sideroxylon* and three paper labels: (1) a primary label that can be no older than 1878 (19 years after Nuttall's death), as it identifies the sheet using Gray's combination, *B. lanuginosa* var. *macrocarpa*; (2) Clark's 1940 annotation label, identifying the sheet as *B. reclinata*; and (3) pierced by one of the fragments, a scrap with two handwritings. On the latter was written in pencil: "B. [blank space for a specific epithet]. Fruit large as a small date! Eatable. Geo." According to James Lendemer of PH (pers. comm.), Charles Pickering, a curator of PH and close friend of Nuttall's (Graustein 1967) probably assembled and mounted this material from Nuttall's disorganized and voluminous material at PH, and supplied the annotations in black ink on Nuttall's scrap of a label: the specific epithet "*macrocarpa* Nutt.," the quotation marks surrounding the original penciled text, and the identification of the penciled handwriting as Nuttall's. This label is unquestionably Nuttall's, as it conforms exactly to his practice in

this regard, as described by Graustein (1967). Only the fragment piercing this label, as discussed near the end of the introduction, is a match for Nuttall's description of *B. macrocarpa* and for the specimens cited above, under additional collections examined. Although Nuttall did not specify a type collection, this specimen is housed in the institution where he worked for many years, both before and after the presumptive collection date of 1830. Therefore I designate the fragment at upper left as the lectotype.

HABITAT

The habitat of *Sideroxylon macrocarpum* is sandy, well-drained, and dry-mesic, but apparently not quite dry enough for the partly sympatric *Chrysoma pauciflosculosa* (Michx.) Greene or *Ceratiola ericoides* Michx. to occur. The great majority of occurrences have a well-developed overstory of *Pinus palustris* P. Mill., with fire infrequent enough (or excluded long enough) to permit arborescent oaks to attain flowering size. The latter may include *Quercus margaretta* Ashe ex Small, *Q. incana* Bartr., *Q. laevis* Walt., *Q. marilandica* Muenchh. and/or *Q. hemisphaerica* Bartr. ex Willd.

Sites that seemed otherwise suitable but had been subjected to significant soil disturbance (e.g. chopping and bedding) were usually devoid of the plant, though occasionally a few survivors could be found. The plant's growth form, with the majority of its biomass beneath the litter layer, seems a clear adaptation to episodic fires as well as for conserving water. Some perennials are promoted by root fragmentation due to chopping and other soil disturbances associated with currently prevalent forestry practices. *Sideroxylon macrocarpum* clearly does not tolerate these practices well.

Aside from *Pinus palustris* and the oaks listed above, the tree most frequently recorded in association with *Sideroxylon macrocarpum* was *Prunus serotina* Ehrh. Shrubs or woody vines recorded as common associates of *S. macrocarpum* were *Licania michauxii* Prance, *Morella cerifera* (L.) Small, *Opuntia humifusa* (Raf.) Raf., *Gelsemium sempervirens* (L.) St. Hil., *Toxicodendron pubescens* P. Mill., and *Vitis rotundifolia* Michx. Frequent herbaceous associates included *Aristida stricta* Michx., *Baptisia perfoliata* (L.) R. Br. ex Ait. f., *B. lanceolata* (Walt.) Ell., *Eriogonum tomentosum* Michx., *Cnidoscolus stimulosus* (Michx.) Engelm. & A. Gray, *Pteridium aquilinum* (L.) Kuhn, *Tephrosia virginiana* (L.) Pers., and *Vernonia angustifolia* Michx. (data from Allison 2000).

Exceptions to the preceding habitat characterization include powerline rights-of-way and road shoulders, where the plant grows in more exposed situations. Here the adverse, drying effects of more sunlight reaching the substrate are apparently counterbalanced by a regular mowing or bush-hogging regime. The latter must surely have much more impact on taller competitors than on the low-growing *Sideroxylon*, promoting its persistence and increase as a result of decreased competition.

COMPARISONS WITH RELATED TAXA

Whether called *Bumelia* or *Sideroxylon*, the temperate species of the southeastern states have long been considered a natural group. Pennington (1990) states that "they are easily distinguished from all Neotropical species by the combination of fascicled leaves with conspicuously finely reticulate tertiary venation, short-styled flowers, small fruit, and the seed with a bipartite scar." Reflecting this, the five such species recognized by him (*S. lanuginosum*, *S. reclinatum*, *S. thornei*, *S. tenax*, *S. lycioides*) are separated, under the first couplet, from all others in his key to the species of *Sideroxylon*. More than century earlier, Gray (1878, 1886), treating all of these taxa except the then-undescribed *thornei*, emphasized the deciduous leaves and "staminodia nearly as large as the proper [medial segments of the] corolla-lobes" as unifying characters.

At one time or another, plants of *Sideroxylon macrocarpum* have been confused with each of the abovementioned species except *S. tenax* and *S. lycioides*. In fact, as discussed earlier, it is most similar not to any of these but to a less well known taxon completely ignored by Pennington, the one now known as *S. rufohirtum*.

Sideroxylon tenax and the closely related *S. alachuense* stand apart from all these species most conspicuously by their densely sericeous-tomentose lower leaf-surfaces, the pubescence mostly tawny or rufous in the former, mostly silvery in the latter. *Sideroxylon lycioides* differs from all except *S. reclinata* s. str. in having leaves that are normally glabrate beneath; the former has consistently larger leaves and fruit than the latter. *Sideroxylon macrocarpum* is readily distinguished from these two taxa by the leaves persistently, if rather sparsely, strigose beneath and by occurring in better drained, sandier habitats than is normal for them. However, populations of *S. reclinatum* from south peninsular Florida, described (Whetstone 1985) as *Bumelia reclinata* var. *austrofloridensis* Whetstone, are more similar to *S. macrocarpum* in having persistent leaf-pubescence; but the small fruit size (≤ 9 mm long) and staminodes equaling or exceeding the corolla-lobe appendages, indeed indicate closer affinity to *S. reclinatum* s. str. than to *S. macrocarpum*.

It seems unlikely that Gray had ever seen material of *Bumelia macrocarpa* when he reduced it to a variety of *B. lanuginosa*, but he probably felt that the persistent foliar pubescence emphasized by Nuttall ruled out synonymizing it under *B. lycioides* or *B. reclinata*. Perhaps Nuttall's use of the term "lanuginous" to describe the vestiture influenced Gray to place it with *B. lanuginosa* and not *B. tenax*. *Sideroxylon lanuginosum* is clearly a heterogeneous taxon, especially as regards coloration, density, and persistence of foliar pubescence, with three subspecies accepted by Pennington (1990). Only *S. lanuginosum* s. str. is known from Georgia or Florida, however, and like *S. tenax*, *S. lanuginosum* subsp. *lanuginosum* has lower leaf surfaces with a persistent pubescence dense enough

to obscure all or most of the laminal surface, while in *S. macrocarpum* and *S. rufohirtum* the hairs are much sparser, the majority of the surface always visible once the leaves are fully expanded. Among the other subspecies of *S. lanuginosum*, only subsp. *rigidum* (A. Gray) Pennington invites comparison with *S. macrocarpum*, by virtue of its small leaves with a foliar pubescence sometimes resembling that of the Georgia endemic. The fruit of *S. lanuginosum* subsp. *rigidum* is unknown to me; however, this plant of the southwestern U.S.A. and northern Mexico is a "shrub or small tree to 8 m" (Pennington 1990).

No doubt the similarity of foliar pubescence was largely responsible for Cronquist's confusion of specimens of *Sideroxylon macrocarpum* with *S. thornei*. While these species do share a similar pubescence and comparatively large fruit size, they exhibit major differences in habit and habitat. *Sideroxylon thornei* is a larger-leaved (to as much as 13.9 cm long [Anderson 1996]), erect and potentially tall shrub or small tree of wetlands, usually associated with *Taxodium*, whereas *S. macrocarpum* is a small-leaved (rarely to 5.2 cm), sprawling shrub less than a meter tall, adapted to well-drained upland woodlands dominated by *Pinus palustris* and various species of *Quercus* L.

As stated previously, *Sideroxylon macrocarpum* is more similar in habit and habitat to the allopatric *S. rufohirtum* than to any other species. They differ in several minor respects and in at least two major ones, androecium (including staminode) size and seed coloration, as indicated in Figure 2 and Table 1.

The known ranges of *Sideroxylon macrocarpum* and *S. rufohirtum* are separated by roughly 190 km (120 miles). Most of this intervening territory is inhospitable to species requiring well-drained soils, as it consists (or consisted, prior to human alteration) largely of lowlands, wetlands and bodies of water, most conspicuously the Okefenokee Swamp. A change in broad-scale landscape within the gap in the two ranges is apparent at once from an examination of a Georgia landcover map (Canalos & Clover 1993), in which the most abundant cover class assigned throughout the range of *S. macrocarpum* is "cultivated/exposed earth." South of this region the Okefenokee is apparent from a glance at this map, but with closer study an area more than twice its size immediately to its west is also well differentiated. This region remains dominated by forest land, reflecting the area's comparative unsuitability for agriculture, presumably due to its being insufficiently well-drained (Christopher Canalos, pers. comm.).

I consider it likely that these two buckthorns are sibling species, now geographically isolated in large part by the development of the Okefenokee and lowlands to its west. Although the oldest peat deposits from the Okefenokee have been radiocarbon dated at a little less than 7000 years B.P., for many years prior to the period of peat accumulation the landscape there was dominated by freshwater marshes (Cohen et al. 1984). Because the Okefenokee developed in a basin formed during one of the last great transgressions of the Atlantic Ocean over southeastern Georgia, during the very late Pliocene or earliest Pleistocene

TABLE 1. Morphological comparison of *Sideroxylon macrocarpum* and *S. rufohirtum*.

Sideroxylon macrocarpum	*Sideroxylon rufohirtum*
Stems usually copiously thorny; galls rarely observed (e.g. *Allison 12220*, GA)	**Stems** less thorny; often with galls (Godfrey 1988)
Leaves usually narrowly oblanceolate or spatulate	**Leaves** usually broadly but sometimes narrowly oblanceolate, spatulate, etc.
Twig and leaf trichomes mostly whitish or translucent, generally less abundant	**Twig** and leaf trichomes rufous (rusty brown), generally more abundant
Pedicels short, 1–3(–5.5) mm	**Pedicels** longer (1.8–)3–6(–8.5) mm
Sepals unequal (outer 2 shorter), pubescence sparse to moderate	**Sepals** ± equal in length, pubescence moderate to dense
Corolla (3.1–)3.7–4.8 mm; medial lobe-segments broadly obovate, lateral segments relatively narrow	**Corolla** 3.8–5.0 mm; medial lobe-segments relatively narrow, lateral segments broader than in *macrocarpum*
Style 1.0–1.3(–1.5) mm	**Style** (1.5–)1.7–1.9 mm
Ovary glabrous or medially villosulous	**Ovary** covered with hairs
Anthers 1.1–1.3(–1.5) mm, filaments 1–2 mm	**Anthers** 0.7–0.9(–1.0) mm, filaments 1.5–2.1 mm
Staminodes (1.2–)1.3–1.8(–2.0) mm, reaching (1/3–)1/2 to 2/3 the length of the medial corolla-lobe segments and exceeded by the lateral segments	**Staminodes** (1.7–)2.0–2.5 mm, nearly reaching the length of the medial corolla-lobe segments and exceeding the lateral segments; occasionally with sagittate bases
Seed evenly brown	**Seed** variegated (brown and yellowish) at maturity

(Rich 1984), the area was unsuited to plants of well-drained soils for at least several millennia prior to 7000 years B.P. The similarity of the habitats of *Sideroxylon macrocarpum* and *S. rufohirtum* does suggest an alternative explanation: that their comparatively large fruit and low stature resulted from parallel or convergent evolution, and not direct descent from a common ancestor.

Whatever the cause, *Sideroxylon macrocarpum* has been isolated reproductively long enough to consistently exhibit at least one morphological extreme within the temperate species-group endemic to the southeastern U.S.A.: a smaller size of staminode relative to corolla lobe. Since it is further differentiated from the similar but allopatric *S. rufohirtum* by having evenly brown mature seeds rather than variegated ones, I have no hesitation in recognizing the Georgia plants at the level of species.

CONSERVATION STATUS

The range-wide decline of *Pinus palustris*-dominated communities due to fire suppression, conversion to other forest types or to farmland, pasture and, increasingly, residential uses, is too well-documented to require discussion here. Whether *Sideroxylon macrocarpum* as a species has suffered the same degree of decline over the last century, or any decline at all, cannot be shown by my

observations, due to a lack of baseline data. Since populations seem best developed where there is a moderate oak understory, it seems likely that fire suppression, where not too rigorous or prolonged, has benefited mid-successional species like *S. macrocarpum*, at least in some relatively xeric habitats over deep sands. Too short a fire interval, with too-frequent destruction of aboveground biomass, outweighs the benefit of reduced competition. The converse: too-prolonged exclusion of fire from the habitat leads to excessive shading from closing of the canopy and crowding out by non-fire-adapted competitors.

Immediate threats to *Sideroxylon macrocarpum* arise chiefly from conversion of its habitat to short-rotation "industrial" pine plantation. Impacts from current practices include soil disturbance (damage to the deep root system), herbicide use (to kill competitors of pine, such as *Sideroxylon*), and fertilizer application. The latter is of no benefit to plants, like this species, that have evolved adaptations making them tolerant of nutrient-poor soils and giving them a competitive advantage there, while fertilization is distinctly beneficial to broadly-adapted, weedy competitors, both native and exotic.

Another cause for concern is the movement away from mowing as a means of maintaining rights-of-way and toward a dependence on herbicides. As discussed above, mowing can provide a competitive advantage to low-growing species such as *Sideroxylon macrocarpum*. Herbicide use, by contrast, leads to their replacement over time by a few herbicide-resistant species, which would seem eventually to require either a return to mowing or changes to the herbicide regime.

At present, as the many collections cited above from the last two decades attest, the plant is not extremely difficult to find within suitable habitat in the part of Georgia to which it appears to be endemic. However, I suggest consideration be given to amending the list of plants receiving protection under the Georgia Wildflower Preservation Act, to replace *Sideroxylon thornei* with *S. macrocarpum*, for several reasons. For one, as indicated earlier, the apparent intent in listing *B. thornei* was to provide protection to the plant now known as *S. macrocarpum*, the result of mistaken specimen annotations by Cronquist in 1970. Secondly, genuine *S. thornei* is now known to be much more widespread and abundant than was once believed (Patrick et al. 1995; Anderson 1996; Allison 2000), with a fair number of occurrences on public lands. Furthermore, the wetland habitats of *S. thornei* receive protection under the federal Clean Water Act (CWA), without regard to any rare species that may be present. This law affords a much greater level of protection to wetland plants than is provided by state or federal protected species laws, which provide little or no *habitat* protection to plants. The CWA provides no benefit to obligate upland species such as *S. macrocarpum*, part of the suite of longleaf pine associates so famously in decline; it serves instead to channel development away from wetlands and into habitats like those of *S. macrocarpum*. Finally, I believe that each

state wildlife agency should recognize a special responsibility to provide for the welfare of those species found nowhere except within the borders of its state.

Of course, the intention of laws like Georgia's Wildflower Protection Act is to prevent additional species from suffering the same fate as the dodo (*Raphus cucullatus*): extinction. This famously extirpated flightless bird of Mauritius is an especially appropriate example because of the link posited by Temple (1977) between its eradication and the decline there of a congener of *Sideroxylon macrocarpum*, *S. majus* (Gaertn. f.) Baehni (syn.: *Calvaria major* Gaertn. f.). In brief, Temple averred that the *Sideroxylon* was represented by a few trees estimated to be more than 300 years old, despite the regular production of well-formed fruit. He theorized that the supposed absence of reproduction in the *Sideroxylon* was due to the extinction of the dodo, which presumably scarified the seeds in its gizzard after ingestion of the fruit and that this was required for their germination. He tested this by force-feeding seeds of the *Sideroxylon* to domesticated turkeys, after which he extracted some of the seeds from the scat and successfully germinated a few of them.[4]

Whether Temple's hypothesis is correct or not (for a contrary view see Owadally & Temple 1979), it seems possible that the comparatively large fruit size of *Sideroxylon macrocarpum* and of its sibling species, *S. rufohirtum*, reflects natural selection to make the fruit more attractive to another terrestrial animal of conservation concern, the gopher tortoise (*Gopherus polyphemus*). The range of *S. macrocarpum* is nested entirely within the range (mapped in Auffenberg & Franz 1982) of this turtle, which is often syntopic with the *Sideroxylon* today (pers. obs.; Fig. 5). It is probable that, prior to the serious decline of the tortoise, it was a regular associate of the buckthorn in the open, well-drained, sandy habitat required by the plant and favored by the reptile. The low stature of this shrub certainly places its fruit within easy reach of the tortoise, though admittedly this may be a secondary result of selection due to recurrent fires that are thought to be required to maintain ideal habitat for both species. It must also be admitted that fruit size in *Sideroxylon* is probably correlated with seed size, and that the greater storage capacity of larger seeds has survival value in drought-prone habitats. Frugivory by *Gopherus* may not have been the primary selective force promoting lower stature and larger fruit. But it should also be noted that, compared to the species with which they have been confused, the large fruits of *S. macrocarpum* and *S. rufohirtum* more closely resemble a fruit reported to be commonly consumed by gopher tortoises: that of *Serenoa repens* (Bartr.) Small (Breininger et al. 1986). As in *S. macrocarpum* and its relatives, the fruit of this native palm is a black, fleshy, mostly subglobose fruit, most of whose volume is occupied by a single large seed (as figured in Uhl

[4]In 1978 this purported case of coevolution of bird and tree was a subject of one of the celebrated series of essays by the late Stephen A. Gould, *This View of Life*, in the popular scientific magazine *Natural History*.

& Dransfield 1987). Birkhead et al. (2005), analyzing gopher tortoise scat, unfortunately from outside the geographic range of either *S. macrocarpum* or *S. rufohirtum*, reported ingestion by gopher tortoises of the large-seeded fruits of several dicotyledonous genera, including *Asimina* Adans., *Licania* Aubl., and *Prunus* L., and found that such seeds were defecated intact. They concluded that these animals play an important role as dispersal agents for plants with large-seeded fruits in pine savannas of the Southeast. It should also be noted that the gap separating the ranges of *S. macrocarpum* and *S. rufohirtum* (see discussion above, following the table) corresponds roughly to a gap depicted on the generalized range map of *Gopherus polyphemus* appearing in Ernst et al. 1994.

Let us hope that future generations will be able to see—if not the hapless dodo—thriving populations of gopher tortoises, big-fruited buckthorns, and as wide a spectrum as possible of the rest of the incalculable diversity of life-form bequeathed and entrusted to us all. We have the means; it remains to be seen whether we also have the will.

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